Origin of the Gondwana flora

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Gondwana flora can be divided into *Botrychiopsis* (=*Gondwanidium*)–*Nothorhacopteris* Assemblage of Late Carboniferous and *Gangamopteris - Glossopteris* Assemblage of Permian. Th evidence of fossil plants from Gondwanaland - Australia, South America and Southern Africa indicates the presence of intermittent phase of glaciation and interglaciation in Southern Hemisphere during Late Carboniferous. Such fluctuating palaeoclimatic condition with increased humidity and relative warming resulted to the advent of newer plant elements. Thus, the Gondwana flora diffrentiated from global *Lepidodendropsis* flora of Early Carboniferous in Late Carboniferous and prolifeated in Permian with the decreasing stress of glaciation.

Key-words- Origin, Evolution, Late Palaeozoic.

INTRODUCTION

THE Gondwana flora, one of the four floras of the Late Palaeozoic, is distributed in Gondwanaland-India, Australia, Southern Africa, South America, and Antarctica, which is characterized by many endemic genera e.g. *Glossopteris, Gangamopteris, Palaeovittaria, Belemnopteris, Raniganjia, Neomariopteris, Rhabdotaenia, Glossotheca, Eretmonia, Ottokaria, Dictyopteridium, Pantophyllum, Noeggerathiopsis* and *Botrychiopsis*, etc. The term Gondwana was initially used by Medlicott in an unpublished report in 1872 (see Holland, 1926) and was originally proposed for a group of sediments laid down in a primarily fresh-water environment, which was published by Feistmantel in 1876, with the rank of the "Gondwana System".

Since the first record of *Glossopteris* leaves from India and Australia by Brongniart (1828), a great progress on the study of Gondwana flora has been made. However, details of the early evolution of the Gondwana palaeokingdom are unclear, owing to the limited data available from the middle part of the Carboniferous, but it may be related to the development of a palaeoantarctic glaciation (Cleal & Thomas, 1991). Origin of the Gondwana flora is still not clear and it is believed that the knowledge of Carboniferous fossil plants of Gondwanaland is essential to know the origin and development of Gondwana flora.

EARLY CARBONIFEROUS FLORA OF GONDWANALAND

As is known to all, the *Lepidodendropsis* flora of the Early Carboniferous is widely distributed all over the world and has similarities on a global scale. Jongmans (1952, 1954) considered that all Early Carboniferous plant assemblages belonged to the same phytogeographic province on the basis of the worldwide distribution of the genera *Lepidodendropsis, Triphyllopteris* and *Rhacopteris*, etc. Therefore, the term *Lepidodendropsis* flora was proposed by Jongmans (1952, 1954), which dealt with a cosmopolitan flora of worldwide extent of Early Carboniferous. The *Lepidodendropsis* flora is characterized by *Lepidodendropsis, Sublepidodendron, Archaeosigillaria, Sphenopteridium, Rhodeopteridium, Fryopsis, Cardiopteridium* and *Anisopteris*, etc. (Chaloner & Lacey, 1973).

The Early Carboniferous *Lepidodendropsis* flora is known from the Po Series of Spiti, N.W. Himalayas (Gothan & Sahni, 1937; Hoeg *et al.*, 1955) and Kashmir (Pal, 1978; Pal & Chaloner, 1979; Singh *et al.*, 1982). Gothan and Sahni (1937) described a small flora from the Lower Carboniferous of the Po Series of Spiti, namely, *Rhacopteris ovata, Sphenopteridium? furcilatum* and *Sphenotpteris* sp. For a long time after Gothan and Sahni (1937) another collection of fossil plants was made from the Po Series of Spiti (Hoeg *et al.*, 1955), which contained *Rhacopteris ovata, Rhacopteris inaequilatera, Rhacopteris* cf.

circularis, *Rhacopteris* sp. a, *Rhacopteris* sp. b, *Sphenopteridium* sp. a, *Sphenopteridium* sp. b, *Rhodea* (=*Rhodeopteridium*) sp. b, *Sphenopteris* sp., *?Asterophyllites* sp., *?Adiantites* sp. a and *?Adiantites* sp. b. These fossil plants reflect the Early Carboniferous aspect. The Early Carboniferous fossil plants from Kashmir were described by Pal and Chaloner (1979), which were known as *Lepidosigillaria* cf. *quadrata*, *Lepidodendropsis* cf. *sigillarioides*, *Lepidodendropsis* cf. *fenestrata*, *Lepidodendropsis* sp., *Archaeosigillaria* sp., *'Cyclostigma' ungeri*, *Archaeocalamites radiatus*, *Rhacopteris* cf. *circularis* and *Rhodeopteridium tenuis*. Singh *et al.* (1982) also described the Early Carboniferous fossil plants from Kashmir, such as *Archaeosigillaria minuta*, *Lepidosigillaria* cf. *quadrata*, *Lepidodendropsis fenestrata*, *Lepidodendropsis* cf. *peruviana*, *Cyclostigma* cf. *pacifica*, *Rhacopteris ovata*, *Triphyllopteris lescuriana*, *Rhodea* (=*Rhodeopteridium*) cf. *subpetiolata* and *Palmatopteris* cf. *furcata*. Recently Pant and Srivastava (1995) have described Lower Carboniferous plants from Wallarama Spur of Punjab Himalaya. Obviously, the Kashmir flora is a typical *Lepidodendropsis* flora and shows close comparability with the Early Carboniferous flora of the world (Table 1).

In addition, Khanna and Tiwari (1983) reported Early Carboniferous palynoflora from Po Formation in Spiti Valley, Tethys Himalaya, namely, *Leiotriletes*, *Retusotriletes*, *Phyllothecotriletes*, cf. *Tripartites*, *Raistrickia*, *Apiculiretusispora*, *Dibolisporites*, *Corbulispora*, *Microreticulatisporites*, *Retispora*, *Lycospora*, *Densosporites*, *Cristatisporites*, *Crassispora*, *Knoxisporites*, *Cirratriradites*, *Vallatisporites*, *Simozonotriletes*, *Hymenozonotriletes*, *Schulzospora* and *Cingulatisporites*. The palynoflora also indicates an Early Carboniferous age to the upper stratigraphic levels of the Po Formation (Khanna & Tiwari, 1983).

The *Lepidodendropsis* flora of Early Carboniferous are recorded in other Gondwana countries, such as Australia, South America and South Africa. A representative *Lepidodendropsis* flora from Peru of South America was described by Jongmans (1954). The flora contains *Lepidodendropsis devoodgii*, *Lepidodendropsis* cf. *de voogdi*, *Lepidodendropsis steinmanni*, *?Lepidodendropsis (Lepidodendron) lissoni*, *?Lepidodendropsis* sp., *Cyclostigma pacifica*, *Cyclostigma* cf. *pacifica*, *Rhacopteris ovata*, *Rhacopteris* cf. *cuneata*, *Rhacopteris* cf. *circularis*, *Triphyllopteris collombiana*, *Triphyllopteris lescuriana*, *?Triphyllopteris peruviana* and *Sphenopteris whitei* (Table 1). Early Carboniferous plant assemblages from Argentina (Wagner, *et al.*, 1985) and Australia (Rigby, 1973; Wagner *et al.*, 1985) are recorded. In addition, many characteristic genera of Early Carboniferous are distributed in Gondwanaland, such as *Lepidodendropsis*, *Sublepidodendron*, *Archaeosigillaria*, *Archaeocalamites*, *Sphenopteridium*, *Adiantites*, *Rhodeopteridium*, *Eleutherophyllum*, *Leptophloeum*, *Cyclostigma* and *Furqueia* (Cleal & Thomas, 1991).

The above-mentioned facts show that the Early Carboniferous plant assemblages are quite abundant and almost include all typical genera of the *Lepidodendropsis* flora of the world. As pointed out by Pal and Chaloner (1979), "the four well-explored parts of the Gondwana block (India, South America, Africa and Australia) now prove to have had as close a floristic similarity before the Carbo-Permian glaciation, as that shown by the more intensively studied *Glossopteris* flora which succeeded it."

Climatic differentiation was not obvious during the Early Carboniferous. This is a basic condition on which *Lepidodendropsis* flora flourished globally. The *Lepidodendropsis* flora has provided the parent source for four floras of Late Palaeozoic (Late Carboniferous to Late Permian): the Cathaysia, Euramerica, Angara and Gondwana floras.

LATE CARBONIFEROUS FLORA OF GONDWANALAND

In India, the Late Carboniferous was a time of the great glaciation that also covered most of the Gondwana Supercontinent. Therefore, records of Late Carboniferous fossil plants are absent in India. However, *Botrychiopsis* (=*Gondwanidium*), typical element of Gondwana, is reported in Australia, South America and South Africa (Rigby, 1973; Plumstead, 1976; Archangelsky, 1986). *Nothorhacopteis*, *Botrychiopsis* and *Ginkgophyllum* (NBG) association has been found to be characteristic in South America (Srivastava, 1992). *Gondwanidium* (=*Botrychiopsis*), *Buriadia* and *Glossopteris* of the Gondwana type in the Upper Carboniferous flora of Tubarao Series and Santa Catarina of the Parana Basin of Brazil and in San Juan Province of Argentina are reported (Fossa-Mancini, 1940; Dolianiti, 1953, 1954; Archangelsky & Sota, 1966). Cleal and Thomas (1991) cited a number of Late Carboniferous elements from Gondwana continent, such as *Botrychiopsis*, *Bergiopteris*, *Bumbudendron*, *Ginkgophyllum*, *Nothorhacopteris*, *Paulophyton* and *Fedekutzia*, etc. Although Late Carboniferous floral elements of Gondwanaland are poor in composition, they are mostly typical genera of the Gondwana type, which have never been discovered in the Cathaysia, Euramerica and Angara floral provinces. We suggest that the Late Carboniferous flora of Gondwanaland should represent the early stage of the Gondwana flora. The floral assemblage is called the

Table 1. Distribution of characteristic species of Early Carboniferous from Kashmir, Peru and Africa

Species	Kashmir	Peru	Africa
Lepidodendropsis africanum Lejal			+
L. devoodgii Jongmans		+	
L. fenestrata Jongmans	+		+
L. hirmeri Lutz			+
L. liddarensis Pant & Srivastava	+		
L. peruviana (Gothan) Jongmans			
L. rhombiformis Rouvre			+
L. schürmanni Jongmans			+
L. scobiniformis (Meek) Read			+
L. sekondiensis Mensah & Chaloner			+
L. cf. sigillarioides Jongmans, Gothan & Darrah	+		
L steinmani Jongmans			
L. sinaica Jongmans & Koopmans		+	+
?Sublepidodendron fasciatum Jongmans			+
Protolepidodendropsis pulchra Hoeg			+
Pseudolepidodendropsis nigeriensis Rouvre			+
Pseudobumbudendron chaloneri Pant & Srivastava	+		
P. meyenii Pant & Srivastava	+		
Spondylodendron wallaramensis Pant & Srivastava	+		
Archaeosigillaria essiponensis Mensah & Chaloner			+
A. minuta Lejal	+		
A. subcostata Danzé-Corsin	+		
Lepidosigillaria cf. quadrata Danzé-Corsin	+		
Cyclostigma pacifica (Steinmann) Jongmans			
C. sinaica Jongmans		+	
Archaeocalamites radiatus (Brongniart) Stür	+		+
Rhodeopteridium tenuis Gothan	+		
Triphyllopteris collombiana Schimper		+	
T. lescuriana (Meek) Lesquereux	+	+	
Racopteris ovata (Mc Coy)Walkom	+	+	
R. cf. *circularis* Walton	+	+	
Sphenopteridium sp.	+		
Sphenopteris whitei (Berry) Jongmans		+	+

Kashmir : Hoeg *et al.* (1955), Pal & Chaloner (1979), Singh *et al.* 1982), Pant & Srivastava (1995)
Peru : Jongmans (1954)
Africa : Jongmans & Heide (1955), Lejal (1969), Mensah & Chaloner (1971), Rouvre (1984)

Botrychiopsis (=Gondwanidium)- Nothorhacopteris Assemblage of Late Carboniferous.

During the Carboniferous evolving patterns of potentially important radial monosaccate palynotaxa are regarded as chronologically significant event, both in Northern and Southern Hemispheres (López-Gamundi *et al.*, 1993; Vergel *et al.*, 1993; Vijaya & Tiwari, 1992). A few records of Middle to Upper Carboniferous palynoflora are known from South America and Australia (Vergel *et al.*, 1993; Roberts *et al.*, 1993). The palynoassemblages which contain common radial monosaccate pollen (*Potonieisporites, Plicatipollenites*) in association with *Cristatisporites* dominance, are recorded in Argentina (Césari, 1986 Césari & Limarino, 1987; Archangelsky & Cásari, 1986), which indicate the Namurian-Westphalian. The other palynoassemblages

recovered in succession in widely separated areas of Australia and Argentina are of late Westphalian-Stephanian (Balme, 1960; López-Gamundi *et al.*, 1993; Vergel *et al.*, 1993), which contain relatively high incidence of cingulate-zonate spores, such as *Cristatisporites* and *Densoisporites*.

To sum-up, Late Carboniferous megaflora and palynoflora of Gondwanaland contain typical endemic elements, which belong to the Early Gondwana flora. Floral elements of Late Carboniferous are drowsy in relation to the glaciation of this age. By the latest Carboniferous, Glossopteris floral elements from western Argentina (López-Gamundi & Espejo, 1993) flourished gradually in other parts of Gondwanaland - India, Australia, southern Africa, South America and Antarctica along with the decreasing glacial stress (Vijaya, in press).

ORIGIN AND FORMATIVE MECHANISM OF THE GONDWANA FLORA

Raymond (1985) believes that "both poles became cooler at the end of the Early Carboniferous (Namurian A) and that the region bordering Tethys became warmer." Owing to the climatic changes, some obvious changes in floral components of the Cathaysia, Euramerica, Angara and Gondwana continents occurred during the transition from the Early Carboniferous (Tournaisian, Visean and Namurian A) to the Late Carboniferous (Namurian B-C, Westphalian and Stephanian), which resulted in extinctions of many plant genera, such as *Lepidodendropsis*, *Sublepidodendron*, *Archaeosigillaria*, *Archaeocalamites*, *Rhacopteris*, *Triphyllopteris*, *Cardiopteridium* and *Rhodeopteridium*, etc. and these extinctions also included number of other species of lycopods, ferns and pteridosperms of this time (Sun Keqin, 1995, 1996).

In Southern Hemisphere, plant succession was arrested by the glaciation during the Late Carboniferous. However, the catastrophic event did not destroy all the floral elements, some of them could have sustained the lethal conditions and continued their occurrence in hospitable pockets (Srivastava, 1992). The evidence of fossil plants from Australia, South America and southern Africa had indicated that at least some stages of Late Carboniferous were a phase of non-glaciation and an intermittent glaciation in the Southern Hemisphere. Thus, the cycle of glacial advance or glacial retreat seems to be the major causal factor for reflecting the growth and distribution of the Late Carboniferous vegetation in Gondwanaland. Such transitional palaeoclimatic conditions with the increase in humidity and relative warming correspond to the advent of vegetation in some span. Significant changes in plant fossil assemblage, known as floral break are probably related to the onset of major glaciation in the Mid-Carboniferous (Wagner, 1982; Meyen, 1987), that is, the transition from the Early Carboniferous to Late Carboniferous. This floral change involves quantitative variation, and also shows the progressive appearance of new taxa, which lead to more than one floral change (Vijaya, in press). The *Glossopteis* floral elements had their ancestry in the Late Carboniferous flora and the change in climate resulted to evolve a glossopterid rich assemblage in Gondwana countries (Srivastava, 1992). Sun Keqin (1995, 1986) believed that the Cathaysia, Euramerica, Angara and Gondwana floras derived from the same *Lepidodendropsis* flora of Early Carboniferous, but developed in different environments respectively.

Some characteristic genera of the Gondwana flora has already existed in Gondwanaland during the Late Carboniferous (Namurian B-C, Westphalian and Stephanian). These elements include *Botrychiopsis* (=*Gondwanidium*), *Bergiopteris*, *Bumbudendron*, *Ginkgophyllum*, *Nothorhacopteris*, *Paulophyton* and *Fedekurtzia*, etc. (Cleal & Thomas, 1991), which reflected the floral regionalism. The Gondwana flora derived from the globally identical *Lepidodendropsis* flora of the Early Carboniferous differerentiated during Late Carboniferous and developed independently in Late Carboniferous and Permian. Although a few relic elements of the Gondwana flora continued into the basal Triassic, new taxa of Mesophytic had already occurred during this time. The flora of the Southern Hemisphere, reflect cosmopolitan character from Triassic to Cretaceous.

CONCLUSIONS

In Gondwanaland, the known Carboniferous and Permian floras can be divided into *Lepidodendropsis* flora of the Early Carboniferous and the Gondwana flora of the Late Carboniferous– Late Permian. The *Lepidodendropsis-Rhacopteris* Assemblage can be recognized as *Lepidodendropsis* flora of the Early Carboniferous. The *Botrychiopsis* (=*Gondwanidium*)-*Nothorhacopteris* Assemblage of the Late Carboniferous and the *Gangamopteris-Glossopteris* Assemblage of the Permian are associated with the Gondwana flora.

The Early Gondwana flora derived from the *Lepidodendropsis* flora of the Early Carboniferous (Tournaisian, Visean and Namurian A) became distinct in Late Carboniferous (Namurian B- C, Westphalian and Stephanian). The flora diversified and flourished suc-

cessfully with the incoming of new elements of its own during the entire span of Permian.

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